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BIOLOGICAL BULLETIN

ECOLOGICAL SUCCESSION.

IV. Vegetation and the Control of Land Animal Communities.

VICTOR E. SHELFORD.

I. Introduction.

In the preceding papers of this series, we have discussed the succession of animals in two types of aquatic habitats with particular reference to fish. While the data presented are only a minor part of those at hand they have served to illustrate some of the principles of succession in aquatic habitats. Discussion of other aquatic situations would enable us to point out many more important facts but we must now pass to land habitats. To illustrate principles here we might discuss the development of either forest or prairie animal communities on sterile mineral soil or in a filling pond. We have selected the succession of forest animal communities on sterile mineral soil and especially those on sand.

The forest conditions on the sand areas at the head of Lake Michigan were once among the best in North America for the study of the problems at hand and in spite of the fact that they are rapidly disappearing and have already been destroyed in some of the localities where the data here presented were collected, there are still various small areas between Indiana Harbor, Ind., and Sawyer, Mich., which taken together present the chief stages of forest development on sand. There are also localities outside the sand area, in which the later stages are to be found on other soils.

The searching of older literature, for possible statements which anticipate ideas here presented would require years and has not been undertaken in any adequate fashion as yet. Such anticipation of ideas and principles is perhaps to be expected but *organization and development are just at their beginnings.* On the plant side some older literature has been brought to attention. Buffon (1742) discovered that poplars precede oaks and beeches in the development of forest (Cowles, '11). Cowles found that in the Lake Michigan sand area cottonwoods precede pines, pines precede black oaks, black oaks precede red oaks, red oaks are usually followed by sugar maple and beech (Cowles '99, '01, '11; Clements, '05; Shantz, '06; Fuller, '11). We are to present certain representative facts concerning the development or succession of animal communities, accompanying and contributing to the causes of plant succession. The data presented are by no means complete as only a small part of the total number of animal species that might be collected from such a series of localities, has been studied. However the data are *adequate* for the purpose of illustrating principles and methods, and of bringing together some of the recent developments in the study of communities of organisms to focus them on the question as to the best method of obtaining and organizing the data of ecology of terrestrial animals.

II. Localities of Study.

The forest development series might be variously divided for purposes of study. The number of stages and variations that might be recognized is considerable. For the purpose just outlined we have selected five stages. Transition areas are present, but only the most important two, namely those between the first and second and the second and third, have been noted. The stages considered are (1) Cottonwood stage; (1–2) the transition between the cottonwoods and the pines; (2) pine stage; (2–3) transition between the pine and oak or mixed pines and oaks together with open places in the oak areas; (3) black oak stage; (4) red oak stage—the red oak associated with the black oak and white oak in the earlier stages and with the shag bark hickory in the later stages; (5) the beech and maple stage.

1. *Cottonwood Stage.*

The cottonwood (*Populus deltoides*) areas are located near the lake shore and the sand is always more or less shifting and rarely with more than traces of humus. The cottonwoods are usually small trees, scattered over the beach ridge, or the lakeward side of the shore dunes as the case may be. Between them are widely scattered bunches of grasses of which *Calamovilfa longifolia* is the most characteristic species and *Ammophila arenaria* usually common. Scattered individuals of *Artemisia canadensis* also occur. The shrubs, which are still more scattered or local, are the beach plum (*Prunus pumila*) and some of the xerophytic willows (*Salix glaucophylla*).

All localities are indicated on the map, p. 62, by letters used as designated below. Two principal cottonwood stations have been studied. One lies to the east, 1*A*, and one to the west, 1*B*, of Pine, Ind. At these points the cottonwood area is about ten rods wide and reaches inland just beyond the crest of the ridge where the plants of transition come in. (For the arrangement of ridges see Fig. 1, p. 137, of "Ecological Succession II.") Two other less fully studied areas have been visited frequently, viz., 1*C*, at Miller, Ind., and 1*D*, at Dune Park. (See map.)

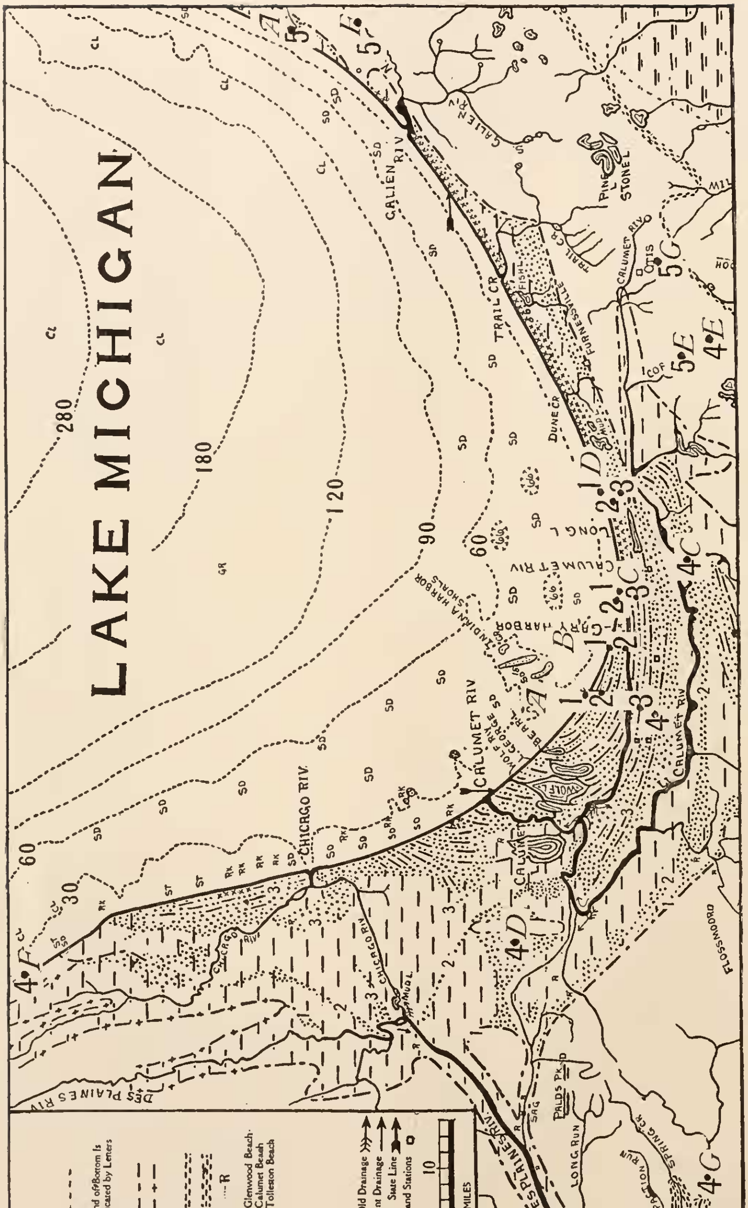

FIG. 1. Map of the area of study. The stations are shown by small dots near the figures. The figures refer to forest stages as follows: 1, cottonwood stage; 2, pine stage; 3, black oak stage; 4, red oak stage; 5, beech stage. The letters standing near are for convenience in reference. *A–D* refer to stages on sand; *E–G* on clayey soil. Fuller has studied evaporation at stations 1, 2 and 3*D* and 5*G* and in the red oak stage at Palos Park.

1–2. *Mixed Pine and Cottonwood Stage.*

These areas lie on the first ridge from the lake. The sand shows traces of humus which is indicated by a slight darkening. The characteristic grass is the bunch grass (*Andropogon scoparius*) which occurs in dense bunches much more closely set than *Calamovilfa* in the preceding. The juniper (*Juniperus communis*), the bear berry and young pines (*Pinus Banksiana*) are the dominant plants, although old cottonwoods and scattered individuals of all the plants of the preceding stage are present. Two such stages were studied.

2. *Pine Stage.*

The sand here is stable and considerably blackened by humus except in blowouts where the wind keeps it constantly shifting. The trees are scattered stunted pines (*Pinus Banksiana*). The large areas of sand are covered with the recumbent bear berry; scattered specimens of many of the herbaceous plants of the earlier stages are to be found. The New Jersey tea (*Ceanothus americanus*) and the juniper are among the most characteristic shrubs. The cactus (*Opuntia Raffinesquii*) occurs in the older stages only. Three stations have been studied; two, 2*A*, and 2*B* (adjoining 1*A* and 1*B*) and 1*D*, at Dune Park, Ind.

2–3. *Mixed Pines and Black Oaks.*

The transition area between pine and oak is characterized by the presence of seedlings of the oak, the choke cherry, the fragrant sumac and an abundance of cacti and Liatris. The ground is much darkened. Herbs are much more numerous than earlier but bare spots of relatively clear sand continue, even after the oaks have entirely displaced the pines. Such transition areas proper have been so much disturbed that only the open bare sandy places in the oak areas are here considered as belonging under this head.

3. *Black Oak Stage.*

We now find the sand to be much darkened by humus and locally covered with a dry moss or with dead leaves. Grasses also partly cover the ground. The shrubby undergrowth is made up of blueberry, choke cherry and New Jersey tea. The oaks (*Quercus velutina*) constitute a much thicker stand than the pines but the type which we are considering here has the open places grassy and covered with a growth of vetch (*Tephrosia virginiana*), golden-rod and other Compositæ. The chief points of study were 3*A*, at Miller, Ind., 3*B*, near Clark, Ind., and 3*C*, at Dune Park.

4. *Red Oak Stage.*

This was originally the most abundant type of forest near Chicago but areas which have not been disturbed by man are few in number. On the sand, hickories are rare. The forest is usually made up of black oak, red oak, and white oak. This is true at 4*A*, 4*C*, and 4*D*, of the map. The more mesophytic type is made up of white oak, red oak, and hickory, with the red oak and the hickory dominating. Our type four then, represents a range of conditions. All the stages are included here and all are characterized by the absence of bare sand and other mineral soil, and by the presence of a carpet of leaves and humus which covers the ground. There is a well marked shrubby and herbaceous growth. The characteristic shrubby species, are blueberry, *Viburnum*, *Cornus*, and *Crataegus*. The shrubs are usually quite numerous and make thick stands locally in the forest. The places studied are, 4*A*, at Hessville, Ind., 4*C*, at Liverpool, Ind. and 4*D*, at Beverly Hills in Chicago. These represent white oak, red oak, and black oak on sand. 4*E*, 4*F* and 4*G*, represent areas on till clay which are in something like primeval conditions.

5. *Beech Stage.*

This type is characterized by beech and sugar maple. The mineral soil is covered with several centimeters of humus and a very thick layer of leaves which is often matted together by fungus hyphæ. The number of species of trees is smaller but the number of species of small shrubs is greater than in the preceding stage. The number of individual shrubs however is smaller. Here the trees close the over-head spaces and make a dense shade, while the lower forest is open. The localities of study are, 5*A*, at Sawyer, Mich., on sand, 5*C*, at Woodville, Ind., now destroyed, 5*F*, at Sawyer, Mich., and 5*G*, at Otis, Ind., on clay

III. Presentation of Data.

We will begin with the animals of the earliest forest stage and proceed to those of the latest. For purposes of comparison animals must be divided into groups with comparable habitat relations. Warming's ('09, p. 138) division into strata may be employed (see Dahl, '08, p. 11). In any locality we note that there are several levels which may be occupied by animals. Some animals live below the surface of the ground and constitute the *Subterranean stratum*. Others live at the surface of the ground and constitute the *Ground stratum*. Animals inhabiting the herbaceous vegetation, and low shrubs, etc., make up the *Field stratum*. Those living on the shrubs and young trees make up the *Shrub stratum*, and those on the trees, the *Tree strata*. Such a division is essential to any comparison of the animals of different forests, steppes, etc. The ground stratum of one cannot well be compared with the field stratum of another; like strata must be compared.

Many animals invade several strata in connection with their various activities. They should, however, be classed primarily in the stratum in which they breed and secondarily in the stratum or strata in which they feed or forage. The breeding activities are of especial importance to the animals in question, while the feeding and foraging influence other animals. The study of the lower strata of the forest presents no difficulties. The tree stratum however is usually far enough above the ground to make observation difficult. The data at hand are rather incomplete at this point and accordingly the discussion is confined to the lower strata.

Tables I. and II. and the lists following them show the distribution of about 200 species of animals in the forest stages. These tables and lists include chiefly animals that have been encountered in these situations often during several seasons. Where collections are known not to have been representative, they are omitted. For example most of the Diptera collected were pre-

Table I.

Showing the distribution of the animals belonging to the subterranean and ground strata of two or more of the animal communities of the forest stages indicated by numbers:—1, cottonwood stage; 1–2, mixed pine and cottonwood; 2, pine stage; 2–3, mixed pine and black oak stage and open places in the black oak forest; 3, the black oak stage, in the later stages white oak occurs; 4, stages containing red oak but not beech and maple (the earlier stages are black oak, white oak and red oak and the later stages white oak, red oak and hickory); 5, beech and maple stage which usually contains some basswood. In the numbered columns, the star indicates that a species is present, *F* signifies few, *C* common, *A* abundant. Strata are indicated by letters at the heads of the columns:—*a*, subterranean including rotten logs; *b*, ground; *c*, vegetation; in these columns *F* indicates feeding place; *B* indicates breeding place. Letters in column marked *lit.* refer to literature in the special bibliography.

Common Name.	Scientific Name.	1	1–2	2	2–3	3	4	5	*a*	*b*	*c*	*lit.*
Tiger beetle	*Cicindela lepida* Lee	*C*	*F*						*B*	*F*		*A*
Sand spider	*Trochosa cinerea* Fab.	*C*							*B*	*B*		*B*
Maritime grasshopper	*Trimerotropis maritima* Harr.	*C*	*F*						*B*	*F*		*C*
Tiger beetle	*Cicindela formosa generosa* Dj.	*F*	*C*	*F*					*B*	*F*		*A*
Long-horned grasshopper	*Psinida fenestralis* Serv.	*C*	*C*	*C*	*C*				*B*	*F*		*C*
Burrowing spider	*Geolycosa pikei* Marx.	*C*	*C*	*C*	*C*				*B*	*F*		*B*
Bembex	*Microbembex monodonta* Say	*C*	*C*	*C*	*C*				*B*	*F*	*F*	*C*
Bembex	*Bembex spinolæ* Lep.	*F*	*C*	*C*	*C*				*B*	*F*	*F*	*D*
Termite	*Termes flavipes* Koll.	*C*	*F*	*F*	*F*	*F*			*B*			*E*
Wasp	*Dielis plumipes* Dru.		?	*	*				*B*	*F*	*F*	*F*
Digger wasp	*Anophilus divisus* Cress.		*C*	*C*					*B*	*F*	*F*	*D*
Sand locust	*Agenotettix arenosus* Han.		*	*					*B*	*F*		*C*
Ant	*Lasius niger americanorum* Em.		*C*	*F*					*B*	*F*	*F*	*I*
Mottled sand locust	*Spharagemon wyominganum* The.		*C*	*C*	*C*				*B*	*F*		*C*
Migratory locust	*Melanoplus atlanis* Ril.		*C*	*C*	*C*				*B*	*F*		*C*
Tiger beetle	*Cicindela scutellaris Lecontei* Hald.		*F*	*C*	*C*				*B*	*F*		*A*
Locust	*Melanoplus angustipennis* Dod.		*C*	*C*	*C*				*B*	*F*	*F*	*C*
Sixlined lizard	*Cnemodophorus sexlineatus* Linn.		*F*	*C*	*C*				*B*	*F*		*H*
Andrenid	*Auglochlora confusa* Rob.			*	*				*B*	?	*F*	*J*
Parasitic bee	*Epeolus pusillus* Cress.			*	*				?	?	*F*	*J*
Burrowing bee	*Spechodes dicroa* Sm.			*	*				*B*	*F*	*F*	*D*
Ammophila	*Ammophila procera* Klg.			*F*	*C*	*F*			*B*	*F*	*F*	*D*
Ant lion	*Mymeleon* sp.?				*	*				*B*		

TABLE I (*continued*).

Common Name.	Scientific Name.	1	1–2	2	2–3	3	4	5	*a*	*b*	*c*	*lit.*
Flat larvæ	*Pyrochroidæ*			*F*	?	*F*	*C*	*C*	*B*			*L*
Snails	*Zonites arborens*			*F*	*F*	*F*	*C*	*F*	*B*			*P*
Centipede	*Lithobius* sp.			*F*	?	*F*	*C*	*C*	*B*			
Eyed elater	*Alaus oculatus* Lin.					*F*	*C*	*C*	*B*			*L*
Borer	*Orthosoma brunneum* Forst.					*F*	*C*	*C*	*B*			*L*
Tree frog	*Hyla pickeringii* Hol.					*F*	*C*	*C*		*F*		*M*
" "	*Hyla versicolor* Lec.					*C*	*F*			*F*		*M*
Snail	*Polygyra thyroides* Say.					*F*	*C*	*F*	*B*	*F*	*F*	*N*
Sow bug	*Porcellio rathkei* Brandt					*F*	*C*	*C*	*B*			*O*
Snail	*Pyramidula alternata* Say.						*C*	*C*	*B*	*F*		*P*
Snail	*Circinaria concava* Say.						*C*	*C*	*B*	*F*		*P*
Sow bug	*Cyclisticus convexus* De G.						*	*	*B*	*F*		*O*
Centipede	*Lyasopetalum lactarium* Say.						*	*	*B*			*Q*
Centipede	*Geophilus rubens* Say.						*	*	*B*			*Q*
Millipede	*Fontaria corrugate* Wood.						*C*	*F*	*B*			*Q*
Millipede	*Spirobolis marginatus* Say.						*C*	*C*	*B*			*Q*
Slug	*Philomycus carolinensis* Bosc.						*C*	*C*	*B*	*F*		*P*
Snail	*Pyramidula solitaria* Say.								*B*	*F*		*O*
Beetle	*Galerita janus* Fabr.						*C*	*C*	*B*	*F*		*L*
Melandrydæ	*Penthe promelia* Fabr.						*C*	*	*B*			*L*
Burying beetle	*Silpha surinamensis* Fabr.						*C*	*C*	*B*	*F*		*L*
Harvestman	*Liobromum nigripalpi*						*	*				
Ant	*Camponotus hereculeanus pennsylvanicus* De G						*C*	*C*	*B*	*F*	*F*	*I*
Beetle	*Cerchus piceus* Web.							?	*B*	*F*		*L*

served in alcohol and only a few of these could be identified. The flies from one station were pinned and accordingly were all identified so that the inclusion of these in the tables and lists would introduce error. The lists and tables are divided into two groups; the first includes the inhabitants of the ground and subterranean strata, the second of the field, shrub and tree strata.

List of Animals Recorded in the Ground and Subterranean Strata of the Stages Indicated only.

In the first column are common names and in the second scientific names. In the third column *B* indicates breeding; *F*, feeding; *H*, hibernating of animals on the situation indicated in column 4 following. Letters in column *lit.* refer to literature cited in the special bibliography at the end of the paper. Statements made on the authority of others are in italics, those starred are by A. B. Wolcott.

Pine Stage.

1	2	3	4	*lit.*
Bee (Andrenidæ)	*Halictus melumboni* Rob.	*B?*		*J*
Larridæ	*Tachytes texanus* Cres.			*F*
Scoliidæ	*Plesia interrupta* Say			
Ampulicidæ	*Anophilus marginatus* Say		In sand	*F*
Beetle (Elateridæ)	*Cardiophorus cardisce* Say		On sand	*L*
Blue racer	*Coluber constrictor* Lin., Var.	*B*	In sand	*R*
Ground squirrel	*Spermophilus 13-lineatus* Mitch.	*B*	In sand	*S*
Elateridæ	*Alaus myops* Fabr.	*B?*	Under pine bark	

Black Oak Stage.

1	2	3	4	*lit.*
Elateridæ	*Lacon rectangularis* Say	*B*	Under Opuntia	*
Erotylidæ	*Languria trifasciata* Say	*B*	Under Opuntia	*
Coral winged locust	*Hippiscus tuberculatus* Beau.	*B*	In sand	*C*
Parasitic bee	*Cœlioxys rufitarsus* Smith	*B*	Bee nest	*R*
Psithyridæ	*Psithurus* sp.			
Eumenidæ	*Odynerus anornis* Say			
Hog-nosed snake	*Heterodon platirhinos* Latr.	*B*	In sand	*R*

Red Oak Stage.

1	2	3	4	*lit.*
Green tiger beetle	*Cicindela sexguttata* Fabr.	*B*	In soil	*A*
White-faced hornet	*Vespa maculata* Lin.	*H*	Rotten wood	*G*
Andrenidæ	*Augochlora pura* Say			
Ant	*Lasius umbratis mixtus aphidicola* Walsh	*B*	Log	*H*
Ant	*Camponotus ligniperda* Latr. *noveboracensis* Fitch	*B*	Log	*H*
Ground beetles	*Pterostichus sayi* Brulle	*B*	Rotten log	*L*
Tenebrionidæ	*Meracantha contracta* Beau.	*B*	Rotten log	*L*
Tenebrionidæ	*Uloma impressa* Mels.	*B*	Rotten log	*L*
Scarabæidæ	*Geotrupes splendidus* Fabr.	*B*	Rotten log	*L*

Staphylinidæ	*Staphylinus violaceus* Grav.	*B*	Rotten log	*L*
Elateridæ	*Melanotus communis* Byl.		Rotten log	*L*
Slug	*Pallifera dorsalis* Bin.	*B*	Log	*P*

Beech Stage.

Frog	*Rana sylvatica* Le Conte	*F*	Ground	*M*
Salamander	*Plethodon cinereus* Gr.	*BF*	Under leaves	*H*
Snail	*Polygyra inflecta* Say	*BF*	Leaves and log	*P*
Snail	*Polygyra oppressa* Say	*BF*	Leaves and log	
Snail	*Polygyra fraudulentia* Pil.	*BF*	Leaves and log	*P*
Snail	*Polygyra palliata* Say	*BF*	Leaves and log	
Snail	*Pyramidula perspectiva* Say	*BF*	Leaves and log	*P*
Snail	*Pyramidula solitaria* Say	*BF*	Leaves and log	*P*
Ground beetle	*Pterostricus corecinus* Newm.	*BF*	Leaves and log	*L*
Beetle	*Xylopodus saperaioides* Oliv.	*B*	Under bark	*LV*

The distribution of the animals of the field shrub and lower tree strata are shown in Table II. and the lists which follow.

Table II.

Showing the distribution of animals recorded from the vegetation in more than one of the animal communities of the forest stages indicated by numbers: 1, the cottonwood stage; 1–2, mixed cottonwood and pine stage; 2, pine stage; 2–3, mixed pine and oak stage and open places in the oak forest; 3, black oak stage, in its later phases white oaks occur; 4, stages containing red oak but not beech and maple; 5, beech and maple stage.

Common Name.	Scientific Name.	1	1–2	2	2–3	3	4	5
(*a*) Spider (Thomisidæ) .	*Philodromus alaskensis* Key	*	*	*				
(*b*) Butterfly	*Anthocharis genuita* Fabr. .		*	*	*			
(*c*) Spider (Epeiridæ) . . .	*Epeira domocilorum* Hentz		*	?	?	?	*	*
(*dd*) Dusky plant bug . . .	*Lygus pratensis* Lin.			*	*			
(*d*) Phasmidæ	*Diaphoromera femorata* Say.					*	*	
(*e*) Assassin bug	*Diplodus* sp.					*	*	*
(*f*) Spider (Thomisidæ) .	*Misumessus asperatus* H		*			*	*	*
(*ff*) Spider (Dictynidæ) .	*Dictyna foliacea* Hentz.					*	*	*
(*g*) Spider (Epeiridæ) . . .	*Epeira gigas* Leach						*C*	*F*
(*h*) Spider (Theridiidæ) .	*Theridium frondeum* Hentz						*	*
(*i*) Bug	*Acanthocephala terminalis* Dall						*	*
(*j*) Stink bug	*Nezara hilaris* Say						*	*
(*k*) Stink bug	*Podisus maculiventris* Say . .						*	*

The letters below at the left refer to the species opposite which they stand in Table II. and the numbers refer to the forest stages as at the heads of the columns of Table II. The capitals and italics have the same meaning as in the preceding table and list (Table I.).

a—from cottonwoods and juniper (1, 1–2, 3) (*B*, *K*).
b—from *Arabis lyrata* (*S*).
c—from pine and herbaceous vegetation (*B*) (4) (*K*).
d—from the trunks of various trees.
e—from black oak (3), red oak (4) and from maple (5).
f—Monarda (2–3) and black oak (3) maple (5) (*B*, *K*).
ff—*F* Monarda (3) (*K*).
g—from undergrowth (4) and beech (5) (*K*, *B*).
h—from shrubs (4) and young beech (5) (*B*, *K*, *T*).
i—shrubs (4) and maple trunk.
j—from red oak trunk (4) and beech trunk (5) (*Linden*, *Citrus*, *Gossypium U*).
k—? (4) and beech leaves (5) (*predaceous U*).
dd—herbs (*W*).

The food plant records in the literature are of no great significance ecologically because the character of the leaves of trees growing in open places and in forest and the physical conditions surrounding them are so different that a species feeding on a given tree in the forest might not feed on the same tree in the open and vice versa.

List of Animals Recorded from the Field, Shrub, and Tree Strata of the Forest Stages Noted.

All columns and symbols as in the list following Table I.

Cottonwood Stage.

1	2	3	4	*Lit.*
Chrysomelid beetle	*Disonycha quinquevittata* Say	*B*, *F*	Willow	*L*
Long-horned borer	*Plectodera scalator* Fab.	*B*, *F*	Cottonwood	*L*
Gall aphid	*Pemphigus populicaulis* Fitch	*B*, *F*	Cottonwood	*Z*
Gall aphid	*Pemphigus vagabundus* Walsh	*B*, *F*	Cottonwood	*Z*

Pine Stage.

Leaf beetle	*Nodonota tristis* Oliv.	*F*	Herbs	*L*, *V*
	Bassareus lativittis Germ.	*F*	Herbs	
Spider (Thomisidæ)	*Xysticus formosus* Banks		Juniper	*R*
Spider (Attidae)	*Dendryphantes octavus* Hentz		Juniper	*Y*, *B*, *K*
Spider (Theridiidæ)	*Theridium spirale* Em.		Juniper	*B*, *K*
Engraver beetle	*Ips grandicollis* Eich.	*B*, *F*	Pine	*V*
Pitch moth	*Evetria comstockiana* Fern.?	*B*, *F*	Locust	*V*

Black Oak Stage.

Thread-waisted wasp	*Harpactopus* sp.	*F*	Primrose	*D*
Andrenid	*Agapostemon splendens* Lepel	*F*	Primrose	*D*
Spider (Thomisidæ)	*Philodromus pernix* Black	*F*	Herbs	*K*
Spider (Epeiridæ)	*Argiope trifasciata* Forsk.	*F*	Herbs	*K*
Sprinkled locust	*Chlœaltis conspersa* Har.	*F*	Herbs	*C*
Grasshopper	*Schistocera rubignosa* Har.	*F*	Herbs	*C*

Tree cricket..........	*Œcanthus fasciatus* Fitch.	*B, F*	Herbs	*C*
Texas grasshopper.....	*Scudderia texensis* Scud.	*B, F*	Herbs	*C*
Cone-head grasshopper.	*Conocephalus ensiger* Scud.	*B, F*	Herbs	*C*
Meadow grasshopper...	*Xiphidium strictum* Scud.	*B, F*	Herbs	*C*
Stink bug............	*Euschistus variolarius* Pal.	*B, F*	Herbs	*W*
Flower bug...........	*Tripleps insidiosus* Say.	*F*	Herbs	*T*
Fork-tailed larvæ......	*Cerura* sp.	*B, F*	Cherry	*V*
Fulgorid.............	*Otiocerus degeeri* Kirby	*B, F*	Oak	*T*
Flat bug.............	*Neuroctenus simplex* Uhl.	*B, F*	Oak	*T*
Colydiid beetle........	*Ditoma quadriguttata* Say.	*F*	Oak	*V*
Prominent larva.......	*Heterocampa guttivittata* Wlk.	*B, F*	Oak	*V*
Prominent larva.......	*Nadata gibbosa* S. and A.	*B, F*	Oak	*V*
Tree hopper..........	*Telemona querci* Fitch(*monticola*)	*B, F*	Oak	*T*
Coreidæ..............	*Chariesterus autumator* Fabr.	*B, F*	Oak	*T*
Jassid................	*Typhlocyba querci* var. *bifasciata* Gall.	*B, F*	Oak	*T*
Jassid................	*Phlepsius irroratus* Say.	*B, F*	Oak	*T*

Red Oak Stage.

Rove beetle...........	*Tachinus pallipes* Grav.	*B, F*	Mushrooms	*D*
Spider (Clubionidæ) ...	*Anyphæna conspersa* Key.	*F*	Herbs	*B, K*
Spider (Dictynidæ)....	*Dictyna* sp. (juvenile)	*F*	Herbs	*B, K*
Spider (Attidæ).......	*Mævia niger* Hentz	*F*	Herbs	*Y, B, K*
Locustidæ............	*Atlanticus pachymerus* Burm.	*B*	Grass	*C*
Spider (Epeiridæ)	*Acrosoma gracilis* Wal.	*F*	Shrubs	*B*
Spider (Epeiridæ)	*Acrosoma spinea* Hentz	*F*	Shrubs	*B*
Spider (Clubionidæ) ...	*Clubiona* sp.		Shrubs	*B*
Spider (Epeiridæ)	*Mangora maculata* Key.		Shrubs	*K*
Jassid................	*Scaphodius auronitens* Prov.		Shrubs	
Beetle...............	*Odontota nervosa* Panz.		Shrubs	
Bug (Nabidæ)........	*Coriscus annulatus* Reut.	*B*	Shrubs	
Spider (Lyngyphiidæ)..	*Linyphia phrygiana* Kock.		Shrubs	
Cicada...............	*Cicada linnei* S. and G.	*F*	Young maple	
Leaf beetle...........	*Calligrapha scalaris* Lec.	*B F*	Young maple	
Stink bug............	*Euschistus tristigmus* Say.	*B F*	Young maple	
Arctiidæ..............	*Halisdota* sp.	*B F*	White oak	*B*
Oak worm............	*Anisota senitoria* Sm. and Abb.	*B F*	White oak	*D*
White oak gall........	*Andricus semiator* Harr.	*B F*	White oak	*Z*
Tree cricket..........	*Œcanthus angustipennis* Fitch.	*B F*	Red oak	
Katydid..............	*Cyrptöphyllus perspecivius* L.	*B* —	Red oak	
Leaf beetle...........	*Xanthonia 10-notata* Say.	*F*	Red oak	
Prominent larva.......	*Symmirista albifrons* S. and A.	*B* —	Maple	*V*
Prominent larva.......	*Datana anguisii* G. and R.	*B* —	Hickory	
Aph id................	*Phylloxera caryæ-caulis* Fitch	*B* —	Hickory	*Z*

Beech Stage.

Beetle...............	*Boletobius cinctus* Grav.		Mushrooms	
Fungus beetle.........	*Boletotherus bifurcus* Fabr.		Shelf fungus	
Snout beetle..........	*Piazurus oculatus* Say.		Shrubs	

Cercopidæ (bug)	*Clastoptera obtusa* Say.	— *F*	Hic., map., hazel	*T*
Tettiginidæ (leaf hop)	*Gypona octolineata* Fitch.	— *F*	Hic., map., beech	*J*
Leaf hopper	*Jassus oblitururs* Say.	— *F*	Maple	
Ichneumonidæ	*Thalessa atrata* Fabr.	*B* —	Larvæ	*V*
Lace wing	*Crysopa rufialbris*	*B* —	Maple	
Lace bug	*Gargaphia tiliæ* Walsh.	*B* —	Beech	*V*
Ichneumonidæ	*Trogus vulpinus* Cb.	*B*	Larvæ	*D*
Pentatomidæ	*Banasa calva* Say.	*F*	Beech	
Lampyrid beetle	*Podabrus basilaris* Say.	——	Maple	*V*
Lycosidæ	*Wala mitrata* Hentz.		Maple	
Theridiidæ	*Notionella interpres* Cam.		Maple	
Lampyridæ	*Telephorus tubercolatus* Lec.		(*Alder.*)	*L*
Harvestman	*Oligolophus pictus* Wood		Maple trunk	—

IV. Discussion of Data.

An examination of Table I. and the lists of ground and subterranean animals, shows that we have on and under the ground a change in species as we pass from the youngest to the oldest stage of forest development. We note also, where data permit estimation of relative abundance, that as we pass from the youngest to the oldest stage, a species is first few in numbers, then common and later decreasing again. Examination of Table II. and the lists of animals inhabiting vegetation, shows the same phenomenon though the delimitation appears somewhat sharper, possibly because these animals are related to plants and the differences in physical conditions are accompanied by quite different plants.

We note that in general, with the change of conditions accompanying the development of forest upon sterile sand or other mineral soil there is also an almost complete change of animal species. This change is comparable to that associated with the development of a stream (Shelford, '11[1]) and the filling of a pond (Shelford, '11[2] and '11[4]). This change in *mores*, if viewed at the oldest point in the environmental series, is *ecological succession.* For example at station 5*A* where beech forest occurs on sand dunes the cottonwood community has probably been succeeded by the pine community; the pine community by the black oak community; the black oak community by the red oak community which has given way to the present beech community.

This could be discussed as in the cases of the ponds and streams. The discussions already published (l. c.) are sufficient to illustrate the methods and principles. Furthermore the succession of conditions and of the tiger beetles applying to forest development has already been briefly outlined (Shelford, '07). (See Adams, '08, '12.)

V. Causes of Animal Succession and the Control of Animal Communities.

1. The causes of plant succession as summarized by Cowles, '11, may be divided into those related to atmosphere and those related to soil. In the case of animals we recognize also difference in food and materials for abode. *Physical conditions* are believed to be *most* important, as indicated by the great mass of experimental work on animal *behavior*. Representative literature supporting this view is cited in the discussions which follow.

1. *Materials for Abode and Food.*

The former are of great importance. There are the greatest differences between the different forest stages, in this matter. The plants of the later stages are more numerous and the leaves less strongly cutinized, even when the plants belong to the *same* species. The difference in leaf structure may be a factor in limiting the distribution of the phytophaga to a certain part of the range of a species of plant. The leaves, fallen logs, and all conditions in which the animals make their abodes, change as the forest develops. Food has been but little studied and we know little or nothing as to what aspects of the food factor are important. Dahl ('96) has studied the relation of carrion eating animals to their food supply.

2. *Soil.*

Those causes of plant succession which are due to progressive changes of soil, may be briefly summarized from an inspection of the description of stations given above. The chief changes obvious to the eye are an increase of vegetation, of leaf covering and of humus.

(*a*) The last of these changes increases the water holding capacity of the soil, while the other two decrease the evaporation from the soil. The water holding power of different soils is different. It increases with the decrease in size of the soil particles and with the addition of humus which takes up water by imbibition. The amount of water in the soil is usually expressed in terms of per cent. of weight but a soil with 8 per cent. of moisture may not give up water to an organism as readily as another soil with only 2 per cent. It is necessary therefore, to determine the capacity of a soil to retain or give up moisture. This has been determined for a number of soils by Briggs and McLane ('07) and Briggs and Shantz ('12), in terms of what they call the moisture equivalent. The moisture equivalent of a soil is the percentage of water which it can retain in opposition to a centrifugal force 1,000 times that of gravity. This has been determined for a number of soils (l. c., '12, p. 57). The maintenance of turgor in plants is believed to be a purely physical matter. If the roots of a plant are in a mass of soil, the plant gradually reduces the water content until the permanent wilting occurs. The *wilting coefficient* of a soil is the moisture content (in percentage of dry weight) at the time when the leaves of the plant growing in the soil first undergo a permanent reduction in moisture content, as a result of a deficiency of moisture supply. The *moisture equivalent* of a soil is 1.84 times the *wilting coefficient for wheat*, used as a standard plant. Fuller ('12) states that the wilting coefficient of dune sand is about 0.75 per cent. while the usual moisture content of the cottonwood dune sand is two or three times this amount. For the clay soil of the oak-hickory forest, according to McNutt and Fuller ('12) the coefficient is about 8 per cent. These standards of soil moisture indicate the amount of water available to animals through direct contact with the soil or available for evaporation into the air of cavities which they construct for themselves beneath the surface of the soil. The soil inhabiting animals of the cottonwood area live in the presence of a greater amount of available water than do the animals of the oak hickory forest.

(*b*) *Plants and Animals.*—Cowles ('11) mentions the importance of soil bacteria which increase with the increase of the humus, and the development of substances toxic to the plants producing them (Schreiner and Reed, '07). Little is known of the effect of animals upon the soils in which they live but if excretory products ever accumulate in any quantity, they probably have a detrimental effect, especially upon the animals which produce them (Colton '08 and citations). On the other hand, many burrowing animals bury organic material and bring mineral soil to the surface. The digger wasps must add much to the sand by burying many insects for their young. Earth worms appear in the later stages and contribute to soil formation (Darwin). Cowles states further on the authority of Transeau that humus accumulation alters soil aeration.

(*c*) *Temperature.*—Transeau found that the temperature of bog soil and bog water is below that of other soils and waters. This has however not been observed in the case of dry soils. The differences between soil on the beach at Sawyer, Mich., Aug. 19, 1911, at 3.00 P.M. and in the beech woods near at hand was as follows: Air 20° C., upper one half inch of sand of cottonwood area 38°–39° C., sandy soil of beech woods 19°–20° C., a difference of 19° C. The upper one half inch of bare sand goes as high as 47° C. on the hottest days of summer while the soil in the beech woods is probably always a little cooler than the air at the time of the air maximum. Cottonwood soil temperature on the hottest summer days at about 3.00 P.M. has been found to be as follows:

TABLE II.

SHOWING VARIATION OF SAND TEMPERATURE WITH DEPTH AND MOISTURE CONTENT.
AIR 36° C.

	Dry Sand.	Moist Sand
1.25 cm. below surface	47° C.	32° C.
3–4 cm. below surface	38° C.	31° C.
8–9 cm. below surface	35° C.	29° C.
10–11 cm. below surface	33° C.	——
12–13 cm. below surface	32° C.	27° C.
17–18 cm. below surface	30° C.	——

Simultaneous readings in later forest stages were impracticable. Even where exposed to the sun moist sand is kept at a lower temperature by the evaporation.

3. *Atmosphere.*

Conditions at and above the surface of the soil, *i. e.*, in the ground and field strata.

(*a*) *Temperature.*—The above data on the temperature of the surface of the soil may be taken to represent essentially the temperature at the surface as well. There are no records of the temperature at various heights above the ground. Noticeable differences within the height of the trees present, are to be expected particularly in the cottonwood and other early stages where much bare sand is exposed.

(*b*) *Light.*—Animals are either positive or negative to the actinic rays of the spectrum (Congdon, '08, Mast, '11). Considerable work has been done by plant ecologists, on the measurement of light with photographic papers but its bearing on plant problems is questioned by some because the nonactinic portion of the spectrum is most important in the process of photosynthesis. It appears that these measurements are of much greater significance for animals than for plants. Zon and Graves ('11) have brought together the literature and discussed the methods of study (see especially several papers by Wiesner).

The light in the cottonwood stage is more intense than in any other of the habitats that we are to consider. Tests of the light in the beech woods and in the road adjoining, made with a Wynne exposure meter, show the following differences:

Location of Meter.	Time Required to Match Standard Tint.
Beech woods—darkest shadows	1,200 seconds.
Beech woods—medium shadows	180 "
Beech woods—brightest spots	10 "
Road on the north side of woods	3 "

While the above table shows a measurement of the actinic rays only, it indicates that in the beech forest, such rays at least, are diminished in intensity to from 1/3 to 1/400 that of full sunlight. On account of the great amount of reflection from sand, the light in the cottonwood stage is probably double that in the wagon road which is bounded on the south by beech woods and on the north by second growth timber.

(*c*) *Combinations or Complexes of Factors.*—As we have already pointed out (Shelford, '11), the animal environment is a combination of moisture, temperature, light pressure, materials for abode and food, all of which factors taken together constitute a complex of interdependences. These various factors are so dependent upon one another that any change in one usually affects several others. This property of environmental complexes is what makes ecology one of the most complex of sciences, and experimentation in which the environment is kept normal except for one factor, an ideal rarely realized in practice, even under the best conditions.

The efforts of ecologists, geographers, and climatologists have long been directed toward the finding of a method, of measuring the environment, which shall include a number of the most important environmental factors. De Candolle undertook to base the efficiency of a climate, for supporting plants, upon the mean daily temperatures above 6° C., this temperature being taken as the starting point of plant activity. Merriam has followed this lead and calculated total temperatures for many places in North America and made maps and zones based upon such totals. This system however, has been rejected by botanists and plant ecologists on account of much evidence both experimental and observational, which is quite out of accord with this view. The scheme has not been generally accepted by zoölogists outside of the United States Biological Survey. There is practically no evidence of an experimental sort, for the application of such a scheme to animals. Relative humidity has been suggested as an important index (Walker, '03) but does not properly express the influence of atmospheric humidity upon the animal body (Hann, '03, p. 53). The saturation deficit has also been suggested but does not take temperature into account.

1. *Evaporation.*

"The total effect of air temperature, pressure, relative humidity, and average wind velocity upon a free water surface in the shade or in the sun, is expressed by the amount of water evaporated" (Hann, p. 72). Since temperature in the season without frost is directly due to the sun's rays, light is in part included. In our latitude, clouds in summer slightly decrease the air temperature (Hann, p. 72). In winter however the temperature of cloudy days is higher. The strongest light is usually associated with the greatest evaporation. Yapp ('09) found that the rate of evaporation was directly correlated with temperature and illumination, but most closely correlated with relative humidity. From the standpoint of including many factors, the evaporating power of the air is by far the most inclusive and is therefore by far the best index of physical conditions surrounding animals wholly or partly exposed to the atmosphere. It is not however to be expected that it will hold good for all the factors under all climatic conditions, and for this reason, records of light, temperature, pressure, carbon dioxid, etc., should be made.

(*a*) *Effect of Evaporation upon Animals.*—In the case of man some observations have been made. According to Pettenkofer and Voit (fide Hann), an adult man eliminates 900 grams of water from his skin and lungs daily. Of this amount 60 per cent. or 540 grams come from the skin alone and changes in relative humidity of only 1 per cent. cause perceptible changes in the amount of evaporation from the skin. If evaporation from the skin and lungs is diminished, the amount of urine is increased, as in many cases are also the secretions of the intestines. Sudden changes in humidity make themselves felt in sudden increased or decreased blood pressure. The less dilute blood of dry climates operates as a stimulant and increases the functions of the nervous system. The consequences are excitement and sleeplessness (Hann, pp. 56–57).

Little has been done on the physiological effect of evaporation or desiccation upon animals. Various writers have found a loss of water associated with hibernation. Greeley obtained the same results with desiccation as with freezing (Greeley, '01; Bachmetjew, '99; Semper, '79, pp. 182–188). The reactions of animals to an atmospheric humidity gradient has probably never been studied. The chief conclusion to be drawn from the literature is that a high rate of evaporation is advantageous to some animals and decidedly detrimental to others. Attempts to keep insects and spiders which live exposed on the prairie vegetation, near Chicago, in the laboratory in screen cages containing vegetation, usually result in the death of the animals within a few hours. On the other hand, the same species will live in glass jars covered or partially covered with glass plates, long after the vegetation which was placed in with them has turned brown and has soured so that it gives off a bad odor. Special investigation would be necessary to determine the cause of this difference in the death rate, yet difference in the rate of evaporation from the animals' bodies is probably an important factor. After long and careful experimental studies dating far back into the history of plant physiology, plant ecologists have come to the conclusion, that the evaporating power of the air is the most satisfactory index of plant environments.

(*d*) *Evaporation in Forest Animal Habitats.*—Fortunately this has been investigated (Fuller, '11) in the five types of stations, viz., cottonwood, pine, black oak, oak-hickory, and beech. Fuller's first three stations were a little more mesophytic than ours. The data were obtained by using a porous cup atmometer. Evaporation from the atmometer is more nearly like that from an organism than is evaporation from any other device; it was devised by Livingston ('06, '08, '10, '10). It consists of a hollow cup of porous clay 12.5 cm. high, with an internal diameter of 2.5 cm. and a thickness of wall of about 3 mm. It is filled with pure water and connected by means of glass tubing to a reservoir usually consisting of a wide-mouthed glass bottle of one half liter capacity. The water, passing through the porous walls, evaporates from the surface, the loss being constantly replaced from the supply within the reservoir. Readings are made by refilling the reservoir from a graduated burette to a certain mark scratched upon its neck. For convenience in handling a portion of the base of the cup is coated with some impervious substance and before being used in the field, the instrument is standardized by comparing its loss of water with that from a free water surface of 45 sq. cm. exposed under uniform conditions. As a further check against error this standardization is repeated at intervals of six to eight weeks throughout the season (Fuller, '11). In Fuller's work, the bottles were sunk so that the evaporating surface of the instrument was 20–25 cm. above the surface of the soil.

Figure 2 shows the results of a season's study by Fuller. "The graph for the pine dunes is decidedly lower and more regular in its contour than that of the association which it succeeds. Its four nearly equal maxima would indicate that within its limits there was throughout the summer season a continuous stress rather than a series of violent extremes. On the whole it shows a water demand of little more than half of

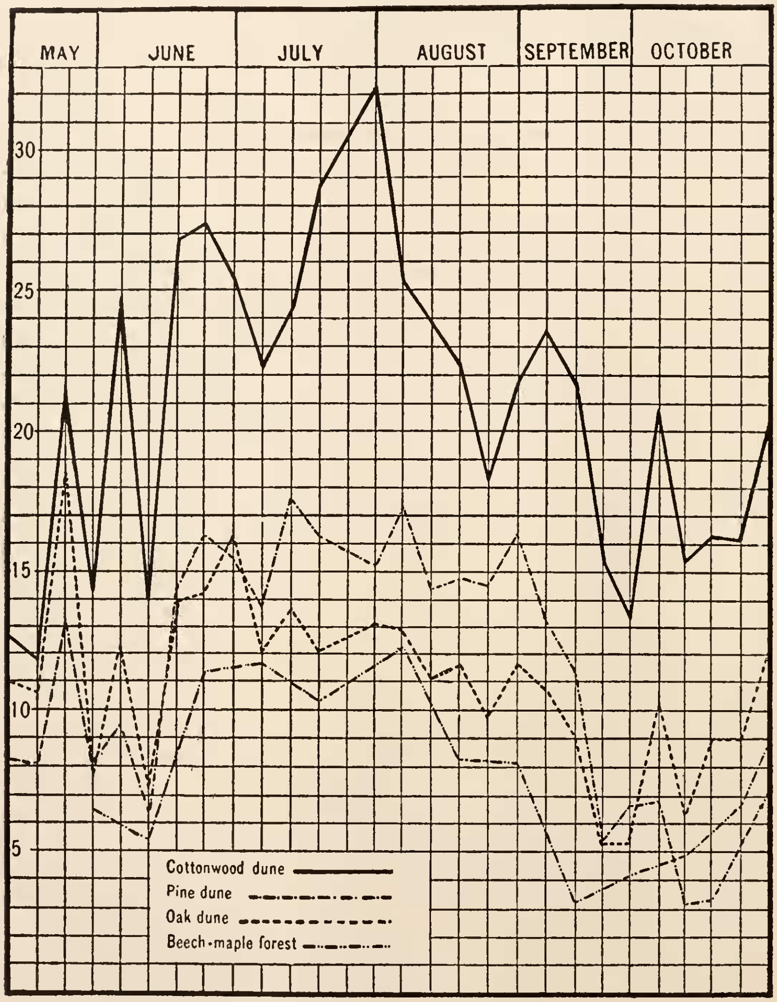

FIG. 2. Mean daily evaporation rates (cc. per day) in the ground stratum of four of the animal communities. (Courtesy of G. D. Fuller and the *Botanical Gazette.*)

that occurring in the cottonwood dunes. Its greatest divergence is plainly due to the evergreen character of its vegetation and is seen on its low range in May and the first part of June, and again in October when it falls below that of the oak dunes and is even less than that of the beech maple forest. This would give good reasons for expecting to find within this association truly mesophytic plants whose activities are limited to the early spring.

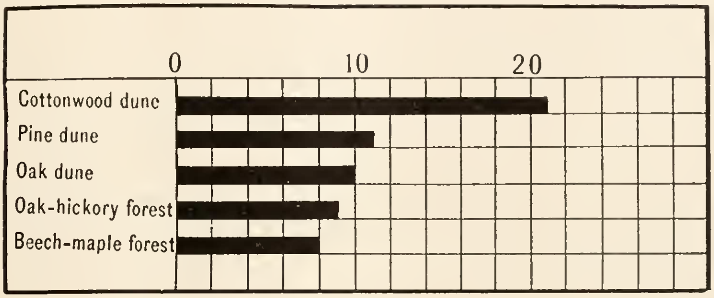

FIG. 3. Showing the comparative evaporation rates (cc. per day) in the ground stratum of the different animal communities from May to October. (Courtesy of Mr. G. D. Fuller.)

Evaporation in the various associations varies directly with the order of their occurrence in the succession (Figs. 3, 4). The differences in the rate of evaporation in the various plant asso-

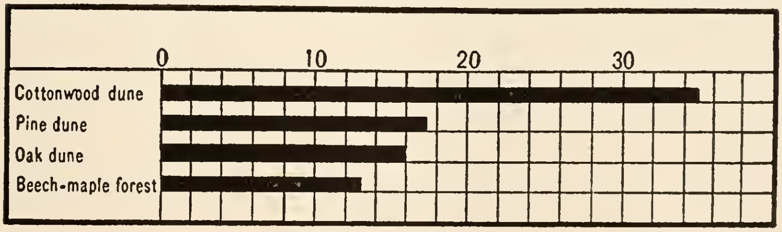

FIG. 4. Showing the comparative evaporation rates (cc. per day) in four of the animal communities on the basis of the maximum amount per day for any week from May to Oct. (Courtesy of Mr. G. D. Fuller and the *Botanical Gazette*.)

ciations studied are sufficient to indicate that the atmospheric conditions are most efficient factors in causing succession." (Fuller, '11.)

A comparison of Fuller's data with the tables and lists of animals shows that the distribution and succession of animals is *clearly correlated* with the *evaporating power of the air*. Further comparison with the description of stations (p. 61) shows that the evaporating power of the air may be taken, in this case, as an index of the materials for abode, etc.

4. *Influence of Physiography and Vegetation upon Animal Habitats.*

In some cases the evaporating power of the air is apparently largely controlled by the vegetation and in others largely by physiographic conditions while as a rule both physiographic conditions and vegetation play important rôles. The importance of the combined effect of physiographic conditions and vegetation is well shown on the steep clay bluffs of Lake Michigan. For example, at Glencoe, Ill., erosion has rendered the bluff steep and brought the ground water near the surface in some places (Shelford, 11[4]). Forest animals occur among the shrubs and under the dead sweet clover (Fig. 5).

TABLE IV.

Showing forest animals in the early stages of forest development of a clay bluff of Lake Michigan. Subterranean and ground strata, 1; bare clay, 2; sweet clover, 3; shrubs, goldenrod, etc., 4; sapling stage; animals same as in 5, the oak-hickory forest.

Common Names.	Scientific Names.	1	2	3	4	5
Tube weaver	*Aglena nævia* Wal.	×	×			
Lycosid	*Pardosa lapidicina* Em.	×	×			
Carolina locust	*Dissostiera carolina* Linn.	×	×			
Mud dauber	*Pelopæus cementarius* Dru.	×	×			
Tiger-beetle larvæ	*Cicindela purpurea limbalis* Klg.	×	×			
Sow bugs	*Porcellio rathkei* Brandt		*F*	*C*	*A*	*A*
Centipede	*Geophilus* sp.		×	×	×	×
Snail	*Polygyra thyroides* Say		×	×	×	×
Snail	*Pyramidula alternata* Say		×	×	×	×
Snail	*Polygyra monodon* Rach			×	×	×
Tiger-beetle larvæ	*Cicindela sexguttata* Fabr.			×	×	×
Snail	*Polygyra albolabris* Say			×	×	×
Slug	*Phylomycus carolinensis* Bosc.			×	×	×
Yellow-margined millipede.	*Fontaria corrugate* Wood			×	×	×
Centipede	*Lyasopetalum lactarium* Say			×	×	×

All of the species beginning with *Geophilus* are commonly found in the oak-hickory forest. On the covered bluff however, where the moisture content of the soil is great and the dense sweet clover and the shrubs make a good covering we find these animals associated with the earliest stages of vegetation development. Shade and moisture here appear to be the determining factors. We note here then that the forest floor conditions are in advance of the forest while on the dry well-drained sand they lag behind in succession.

Some investigators have questioned the importance of vegetation to animals and we note here that the distributions of plant and animal species are not always correlated. If one

FIG. 5. The bluff of Lake Michigan at Glencoe, Ill., showing several stages of forest development. To the right of an imaginary line *a–b* are small areas of the habitats shown in Table IV., in columns 1 and 2. Within the triangle *a–b–c* are areas of the same habitat invaded by shrubs under which are found forest animals. To the left of *a–c* is an area of shrubs and saplings which has a full quota of forest floor animals. (Reprinted from the *Journal of Morphology*.)

refers to *species* of *plants* and *species* of *animals* then the vegetation very often is not correlated with the distribution of the animals. If on the other hand one means that the plants are controllers of physical conditions, then vegetation can be said to be of very great importance.

5. *Stratification of Conditions.*

An inspection of the tables and the discussion following them shows that different animals which do not burrow into the ground inhabit different levels of the forest. For example *Acrosoma* *spinea* Hentz builds its web 1–3 ft. above the ground while *Acrosoma gracile* Wal. builds 4–6 ft. above the ground (see Dahl, '08).

TABLE V.

EVAPORATION FROM POROUS CUP EVAPORIMETERS IN DIFFERENT STRATA OF A SUMMER DRY MARSH, CAMBRIDGESHIRE, ENGLAND, DURING THREE PERIODS BETWEEN JULY 9 AND SEPTEMBER 8, 1907.

(Yapp, '09, p. 299 and 294.)

Year.	Height above Ground.	Ratio of Evapor.	Temperature.			
			Mean Max.	Mean Min.	Mean.	
1907	5 ft. 6 in. to 4 ft. 6 in.	100.00	22.1	6.6	16.5	Well above vegetation.
1907	2 ft. 2 in.	32.8	23.0	—	—	A little above the mid height.
1907	.5 in.	6.6	18.0	7.1	14.1	
1907	soil	——	12.7	11.2	11.8	

The above table shows marked differences in the rate of evaporation, considerable differences in temperature at the different levels and both due largely to vegetation. Differences in light are also to be expected. Sherff ('12, p. 420) has found conditions similar to the above by a two months' study of evaporation on Skokie marsh near Chicago. The evaporation there was three times as great at a height of 1.95 m. as at the surface of the soil in among the plants of Phragmites. Mr. Harvey has also secured similar (unpublished) results on the prairie at Chicago Lawn, Chicago.

It has been long recognized that there are distinct growth-form strata in nearly all plant formations, pelagic algæ formations being a possible exception. The data of Sherff and Yapp indicate differences in conditions in the strata of grass formations and associations. Greater differences are to be expected in the different strata of forests and shrub covered areas. Mr. Fuller informs us that there are marked differences in the structure of leaves at different levels of the same forest tree.

6. *Apparent Anomalous Distribution.*

Are physical conditions sometimes similar when vegetation and landscape aspect are very different? That they are is clearly suggested when we compare the forest and the shrub covered bluff where forest animals occur. Plants grow from seeds only under a very limited range of conditions. However if trees are given a few years' growth under favorable conditions they will be successful under a great range of conditions. The great age to which trees often live and the slowness with which they grow makes it possible for conditions to change while the trees still live on with changes only in leaf structure. It is to be expected that the distribution of animals is correlated with the occurrence of seedlings or of quick growing plants or at least with leaf structure types rather than strictly with species of trees. These facts suggest that there are two types of cases in which physical conditions and forest conditions are not in accord. In the first case atmospheric conditions become favorable for forest animals before any woody plants have been able to grow, in the second, woody plants remain after conditions have become unfavorable for forest animals; both are due to lagging behind of vegetation; both are very local and of minor significance.

A comparison of the data of Yapp (Table V.) and Transeau (Fig. 6) shows a difference between the evaporation of the lower

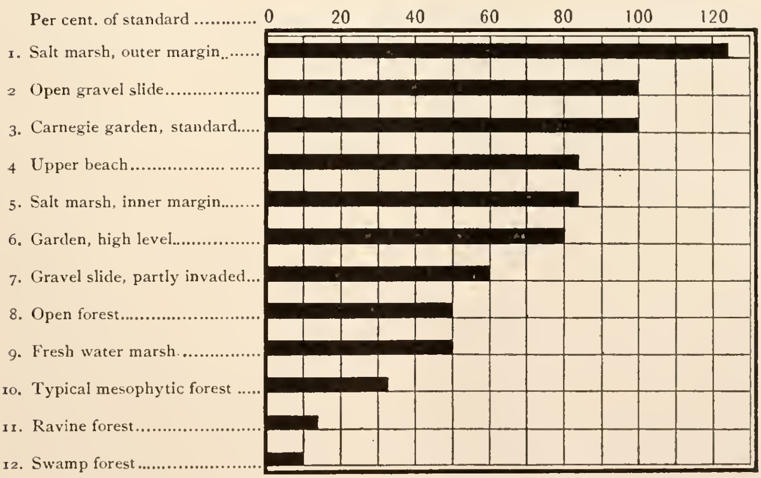

FIG. 6. Showing the comparative evaporation rates (c.c. per day) in the ground stratum of several animal habitats on Long Island during July and August. (After Transeau, courtesy of the *Botanical Gazette*.)

stratum of a marsh and the free atmosphere above, comparable to that found by Transeau between the lowest stratum of the mesophytic forest and the open gravel slide. An inspection of Transeau's data (Fig. 6) on evaporation indicates several obvious cases of similarity; *e. g.*, we note that the rate of evaporation is about the same in the fresh water marsh and the open forest. The data at present available do not justify definite conclusions, yet it may be suggested that there are various stations in strata of the different plant communities where the conditions of the physical factors are essentially identical, but where the necessary materials of abode, especially those used in breeding, are sometimes wanting. Their absence alone is sufficient to prevent animals of specialized habits and structures from taking possession of situations otherwise entirely suitable.

The reasons for the wide distribution of some animals in the forest stages which we are considering are no doubt various. For example *Zonites arborens* (Table I, p. 67) is rare in the early stages and is confined to the lower and moister localities. If *Epeira domicilorum* is a species of stable physiological makeup we can offer no explanation for its peculiar distribution (Table II, p. 69). A species may have its critical period in the early spring when the leaves are off the trees and the condition of the atmosphere similar in all (see Fig. 2) stages or may live at higher levels in the denser and older stages, and thus be surrounded by similar atmospheric conditions, but we are not warranted in assuming either of these causes here.

Another striking feature of the distribution of many beetles, bugs and spiders, and Orthoptera is the fact that they are found in open woods, edges of woods, on the vegetation of marshes and over the water of small ponds in which vegetation is growing. In this way many species are found to occur in what at first appear to be very unlike situations. *Lygus pratensis*, *Tripleps insiduosus*, and *Euschistus variolarius* which occur on the vegetation of the margins of swamps, of the black oak forest dunes and on prairies and agricultural lands may serve as examples. Shull ('11) has pointed out similar facts as one of the difficulties in the way of ecological classification of Orthoptera and Thysanoptera. Such species as the bugs mentioned above are said to occur "everywhere," although they are rarely found in moist woods or in any situation in which they are not fully exposed to the sun and may always live in similar conditions.

There are great differences between open prairies and closed forests. Shimek ('11) found that the evaporation in the undisturbed groves in eastern Iowa during July and August was very much less than that in the prairies adjoining. From the free surfaces of pans set in the ground so that the water which they contained was level with the surface of the soil, the evaporation of the groves was about 27 per cent. of that of the prairie; with cup evaporimeters about 37 per cent. and with Piche evaporimeters about 47 per cent. This is about the same as the difference on Long Island between the inner side of Transeau's salt marsh dominated by grass-like plants and his mesophytic forest. Sherff ('12) found the evaporation in a marsh forest to be a little less than that in the beech maple and from 1.8 to 2.6 times as great as in the lowest stratum of a marsh. While differences and similarities of physical conditions are sufficient to account for many peculiarities of ecological distribution, it must be recognized that the *same species may occur under different conditions and show difference in mores* (Bohn, '09, Allee, '12).

5. *Agreement of Plant and Animal Communities.*

Before discussing the problem of agreement between plant and animal communities, it is necessary to state what is meant by agreement. According to present developments of the science of ecology *plant and animal communities may be said to be in full agreement when the growth form of each stratum of the plant community is correlated with the conditions selected by the animals of that stratum.* Questions of agreement are primarily questions for experimental solution. Two types of disagreement are to be expected. We may illustrate the first by a bog or marsh community. Considering plants rooted in the soil we note that water is secured from the soil by the roots and is lost through the leaves and twigs. Accordingly since bog soil is unfavorable, due to the presence of toxins or to other causes, plants growing in it do not secure water easily even when the quantity of soil water is great. *Such plants have xerophytic structures (which tend to check the loss of water) developed far beyond the requirements of the atmospheric conditions surrounding their vegetative parts.* It is improbable that the animals inhabiting a bog-vegetation field-stratum would *select* atmospheric conditions such as produce equally xerophytic structures under *favorable soil* conditions. We may therefore expect disagreement. The smaller plants such as fungi, algæ, etc., are related to the strata of soil and atmosphere exactly as the smaller animals and as *much disagreement* is to be expected between such plants and the rooted vegetation as between the rooted vegetation and animals. It must also be noted that the xerophytic structures of the plants of *unfavorable* soils may have important influence upon ectophytic plants and animals and in part counteract the effect of favorable atmospheric conditions.

The second type of disagreement is represented by cases in which the vegetation is said to lag behind. We have noted that on the clay bluff, conditions become favorable for inconspicuous plants and forest animals as soon as the growth of the pioneer vegetation gives shade to the soil. In other cases woody vegetation remains in situations where the conditions have become unfavorable for it and the less conspicuous plants and some of the animals have disappeared. We may expect lack of accord within and between plant and animal communities under such conditions. In these cases, however, conditions are only *temporarily out of adjustment*, due to rapid physiographic changes and we note from the data presented that plant and animal communities are usually in agreement. The exceptions are often apparent only and due to the emphasis of *species* instead of *mores* and *growth form*.

VI. General Discussion.

At this point we may note certain aspects of the basis for the organization of ecology into a science. It is possible to characterize the communities of the forest in physiological terms though we cannot be as definite as is to be desired, until *mores* have been studied in detail. Taking the communities one by one and stratum by stratum we may note obvious characters.

A. Pioneer Communities.

The communities of the cottonwood, pine and black oak stages may be designated as pioneer because of the presence of bare mineral soil.

1. *Subterranean and Ground Strata.*—(*a*) The cottonwood community is characterized by animals which breed and spend the dark and cloudy days chiefly below the surface of the sand. They are very largely diurnal and predatory, are exceedingly swift and wary. The burrowing spider (*Geolycosa pikei*) is one of the few nocturnal animals.

(*b*) The pine community is characterized by similar *mores*, but is to be distinguished from the preceding by the presence of many animals which prefer sand that is less shifting and which is slightly *darkened by humus* (Shelford, '07). Animals requiring "cover," such as the lizard, the blue racer, a few ground squirrels, etc., give character because of their absence from earlier and later communities.

(*c*) The black oak community represents the climax of diversity of the subterranean and ground strata. The bare sand *mores* continue in the open spaces, which we have designated as transition areas. Leaf cutters are now present while among the burrowers, the root borers (Prionids and Lucanids) work on the roots of the decaying trees. The behavior differences between this and the preceding communities are differences of detail which, for the making of deductions, would require much careful study.

2. *Field and Shrub Strata.*—The field and shrub strata of the cottonwood, pine and oak communities are less easily characterized. The cottonwoods of the beach are far less commonly infested with aphid galls than are trees of the same species growing in less exposed situations. Furthermore we have never found any of the lepidopterous larvæ such as *Basilarchia archippus* near the beach. Animals living exposed upon the trees are few in number. The same general conditions obtain on and among the pines but spiders are more numerous. On the black oak the number of phytophaga is increased and the number of galls appears to be greater than in the later stages; the inhabitants of the herbaceous vegetation are chiefly those found in

open situations such as prairies and roadsides, where the physical conditions are similar. Some animals of the same species which make up the black oak community were taken from a roadside and after being mixed with the inhabitants of the shrubs of the beech forest, were placed in a light gradient. Soon the insects and spiders of the two communities separated sharply from each other, the beech-inhabiting species going to the darkest end while the roadside species all crowded to the light.

B. Later Communities.

With the coming in of red oak true forest with the mineral soil largely covered with humus and leaves is present and very different *mores* obtain. The diurnal diggers are practically absent. Snails, beetles, grasshoppers, spiders and myriopods living under bark, decaying wood, and leaves, avoiding strong light and requiring moisture, are the chief types. The *mores* are typically forest in character. The differences between these and the later stages are those of detail and degree which need careful study. In general with a lessening in the severity of the conditions, there is a proportional increase in the use of the vegetation as a place of abode.

In the field and shrub strata, we note that the animals of the cottonwood, pine and oak stages are characteristic of open dry situations, requiring or tolerating strong light, while those animals of the red oak, hickory and beech stage are negatively phototactic to light of the same intensity, as shown by mixing the animals in a gradient.

The animals of the tree stratum are few and scattered in the cottonwood, pine and black oak stage while animals enclosed in galls or cases are common if not dominant. In the red oak, hickory and beech stage phytophaga are often gregarious and numerous. The vegetation is used more and more for a breeding place as the forest increases in denseness. Groups such as orthoptera, beetles, bees and wasps, are represented more and more by species which make use of the vegetation as forest development goes on. The tree strata of all the forest stages are characterized by species given to frequenting a limited number of kinds of trees.

C. General Considerations.

We note that the distribution of animal species which occur chiefly on a particular plant species or on closely related species of a group, do *not often occur everywhere* that the plant or plants occur, and if they do there is a marked difference in the number of individuals. Such phenomena appear to be matters of common observation among naturalists. While they are still subjects for investigation, there is much evidence that the local distribution of the phytophaga is not that of the food plant or plants but is limited to a certain portion of the local range of the plant, by differences in the physical conditions, or the growth form of the plant or both. The food plants of phytophaga having a number of food plants are usually those growing in associations. The fauna of trees growing in different communities or under different conditions are probably *commonly different.* The differences in the *mores* of the communities outlined above are clearly correlated with factors known to be of importance in the behavior and physiology of animals. These are materials for abode, soil moisture, light and the condition of the atmosphere.

The more important features of the environment of an animal are selected through its reactions, which are probably innate or instinctive (Wheeler, '10, p. 159; Shelford, '11[4], pp. 556–582; Hancock, '11, p. 327; Herrick, '05, p. 201). Different species usually select different habitats or different strata in the same habitat. It is well known among naturalists and experimenters that *different species* usually have *different mores* (Brehm, '96, p. 73).

Animals of the same species show behavior differences in different habitats (Jennings, '06, Ch. XXI.; Shelford, '11[4], p. 584; Allee, '12). Bohn found, that the sea anemones living near the surface of the sea where the wave and tide action are strongest, showed more marked rhythms of behavior in relation to tide than those living lower down where the action of the tide and waves is less marked (Bohn, '10, p. 156; Holmes, '11, p. 155). These rhythms disappeared slowly when the animals were removed from the tide to the aquarium. Many such cases are probably to be found in the natural history literature. For example the chipmunk differs in behavior under different conditions (Wood, '11, p. 523). Abbot ('70, p. 104) makes a similar statement about fish. It is apparent then that one species may have *several mores* (Bohn, '10 et al.). Different species may sometimes have *identical mores;* these cases are usually separated geographically (Shelford, '11, p. 32; '11², p. 147; '11⁴, p. 604). In addition to these relations, the relation of ecology to species is largely a matter of language, names being necessary as a means of referring to animals.

Animal ecology has very much in common with plant ecology. Diatoms, flatworms and many other marine animals and plants meet the same conditions in the same or similar ways (Loeb, '06, p. 121; Bohn, '10, p. 156; Holmes, '11, p. 155). Sessile animals, such as reef-forming corals, show growth form differences (Woods-Jones, '10) under different conditions, just as sessile plants do. Comparable plants and animals show comparable responses. The physiological life history aspect of plant ecology (Ganong, '07) is parallel with the same phenomenon in animals, but the activities of motile animals correspond roughly to the growth-form phenomena in sessile plants (Shelford, '11⁴, p. 593). Results of study of the environment are equally applicable to plants and to animals. Since *mores* and *growth-form* are correlated with the *environment* much progress can be made by the *study* of the environment; in fact, study of the environment is necessary for progress.

On the other hand the study of the environment must be accompanied by experiments designed to determine the relative importance of the different factor *to animals*, or the results, like so many of our meteorological records, will prove to be of questionable value for the purpose for which they are intended. In the case of the forest animal communities which we have studied, experiments must be undertaken to determine the physiological relations of animals to materials for abode, soil moisture, light and the condition of the atmosphere before the subject can progress beyond the suggestive stage which this paper necessarily represents.

Ecology or ethology of single isolated species is a very old branch of biological study. The developments of the last twenty years have been in the direction of organization of these isolated facts into a science on the basis of *mores*, including *habitat preferences*. The similarities between the response phenomena of plants and animals have led in the direction of the organization of a branch of biological science embracing both plants and animals. It is this organization, or the possibility of organization, which we are attempting to introduce here. The experimental work cited above is adequate to indicate the lines along which further investigation should be directed and that *the mores problem, which includes the habitat preference problem, is the central problem of ecology.*

VII. Summary.

1. The development of forest on sand or other mineral soil is accompanied by an almost complete change of animal *species* and probably by a complete change of animal *mores* (pp. 67–72).

2. Forest development is accompanied by marked changes in soil and physical factors; animal distribution is more closely correlated with differences in *physical factors* than with species of plants (pp. 73–82).

3. For animals living in the soil, the moisture equivalent, or the wilting coefficient for a standard plant, is the best index of the moisture available to the animals (p. 74).

4. The rate of evaporation or the evaporating power of the air is probably the best index of the conditions of the atmosphere (p. 77).

5. The rate of evaporation, temperature, etc., have been found to be very different in the different communities and also different in the different strata of the same communities. The amount of evaporation in animal communities is directly related to their order of occurrence in succession (p. 81).

6. Plant and animal communities are divisible into strata which represent vertical differences in physical conditions. The bodies of many plants occupy several strata but their vegetative parts are usually in some particular stratum. Land animals are comparable to smaller non-rooted plants such as algæ, lichens and fungi. Many animals carry on different activities in different strata, but are to be classed primarily with the stratum in which they breed (p. 84).

7. Succession of all the animals of the forest communities under consideration is comparable in principle to that in ponds. Succession is due to an increment of changes in conditions produced by the plants and animals living at a given point. Animals through their effect upon the soil play an important though minor part in the process (pp. 73, 75).

8. The various animal species are arranged in these communities in an orderly fashion and the *dominating animal mores* are correlated with the *dominating conditions* (pp. 81, 89–90).

9. Taxonomic (structural) species usually have distinct *mores*, though the same species often has different *mores* under different conditions, and different species may have the same *mores*. *Species* and *mores* are therefore not synonymous (pp. 91–92).

10. Ecology considers together *mores* that are alike or similar in their larger characters (p. 92).

Hull Zoölogical Laboratory,
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